A RE-EVALUATION OF THE PLANTS *TINGIA* AND *TINGIOSTACHYA* FROM THE PERMIAN OF TAIYUAN, CHINA

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ABSTRACT. The two characteristic Cathaysian Carboniferous–Permian genera *Tingia* and *Tingiostachya* are reviewed and rediagnosed in the light of new specimens from Taiyuan, northern China. Epidermal features of *Tingia* include bands of longitudinally arranged stomata. *Tingiostachya* is shown to have spirally arranged sporophylls with each bearing one spheroidal sporangium, rather than the previously described whorls of four sporophylls and tetralocular sporangia. *Tingiostachya tetralocularis* and *Tingia elegans* are rediagnosed. The morphological and taxonomic relationships between the two genera are discussed, and it is proposed that a new family Tingiostachyaceae includes *Tingiostachya* and the satellite taxon *Tingia*.

FOUR floras can be recognized in Carboniferous and Permian strata: the Euramerian flora, the Angaran or Kusnezk flora, the *Glossopteris* flora, and the Cathaysian flora (Chaloner and Meyen 1973; Li and Yao 1982, 1983). The Cathaysian flora extended over what is' now China, Korea, Japan, and as far as Sumatra and New Guinea. The flora started to diversify from the Euramerian flora in the late Carboniferous, reached its greatest diversity in the early Permian, and persisted into the late Permian. The Cathaysian flora can itself be divided roughly by the present latitude of 35° N. into two distinct floras, the Northern Cathaysian flora and the Southern Cathaysian flora (Li and Yao 1983).

In the Northern flora, plant assemblages are found throughout the sequence of strata from the late Carboniferous (Stephanian) to the late Permian (Lee 1963, 1964; Li and Yao 1983). Here the late Carboniferous consists mainly of shales, coal-seams, and limestones with the *Neuropteris ovata–Lepidodendron posthumii* assemblage. The assemblage is recognized as the oldest division of the Cathaysian flora because of the presence of *Tingia* and the abundance of distinctive lycophytes. The early Permian Shanxi (Shansi) Series is mainly of terrestrial origin although it includes several thin marine layers with *Lingula* spp. The *Emplectopteris triangularis–Taeniopteris* spp.–*Emplectopteridium alatum* assemblage characterizes this series. Only thin coal seams are present in the overlying Lower Shihezi (Shihhotse) Series and the plants constitute the *Emplectopteris triangularis–Taeniopteris* spp.–*Cathaysiopteris whitei* assemblage. There are no coal seams in the Upper Shihezi Series except in the southern marginal areas and the plant assemblage has changed to what has been interpreted as the main late Cathaysian flora with the major characteristic elements being *Gigantonoclea hallei*, *Fascipteris* spp., and *Lobatannularia eusifolia*.

The plant assemblage sequence in the Southern flora, unlike that of the Northern flora, is discontinuous and the stratigraphic succession is interrupted by volcanic and marine deposits.

The Lower Permian plants described here are from exposures in Simugedong approximately 5 km north-east of East Hill Mine, Taiyuan, Shanxi province, northern China (text-fig. 1). Here the Permian strata are well exposed and widely used as an index section in China. The assemblages of the Northern flora mentioned above were mainly established from work in the Taiyuan area as the local strata contain one of the best-known Lower Permian floras of the northern hemisphere. The main groups of plants previously described from this flora are pteridophytes, cycadophytes, and the Noeggerathiales (including *Tingia* and *Tingiostachya*) with *Tingia* being one of the characteristic genera of this flora.

TEXT-FIG. 1. Map showing distribution of *Tingia* and *Tingiostachya* in south-east Asia. 1, Halle 1925 and 1927, Konno and Asama 1951, and present specimens. 2, Konno, 1929. 3, Stockmans and Mathieu 1939. 4, Bohlin 1971. 5, Konno *et al.* 1971. 6, Feng *et al.* 1977. (1–3 and 6 both genera; 4 and 5 *Tingia*).

MATERIAL AND METHODS

The specimens described here are preserved as compressions and impressions in a grey shale. The irregular surface produced during the splitting of the shale necessitated some *dégagement* of many of the specimens. This was done with the aid of tungsten needles sharpened by heating and subsequently dipping into molten sodium nitrite. Maceration of portions of leaves, sporophylls and sporangia unfortunately gave neither cuticle nor spore coats, so both fragments of the specimens and their impressions were prepared for high-resolution studies by scanning electron microscope. Both 'Silflo' dental rubber and cellulose acetate (nitrocellulose dissolved in amyl acetate) pulls were used to prepare these impressions. Specimens were coated with gold using an Emscope sputter coater prior to examination with a Cambridge S600 Scanning Electron Microscope.

The specimens will be deposited in the Beijing Graduate School, China Institute of Mining, Beijing, China (numbers prefixed by GP).

HISTORY OF RESEARCH

Tingia. This genus was instituted by Halle (1925) for some Permian leafy shoots from northern China, which had previously been described by Schenk (1883) under *Pterophyllum* Brongniart. Halle placed these specimens in a new genus as they had anisophyllous shoots with four ranks of leaves, unlike the simpler two ranked
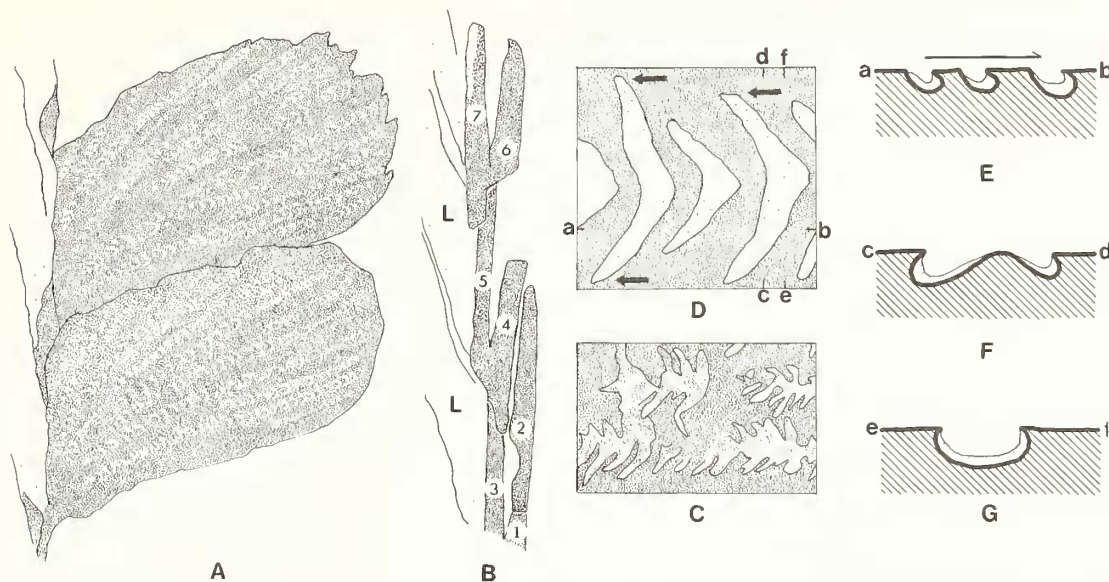
TEXT-FIG. 2. *Tingia elegans* Konno. A, two larger leaves showing lines of crescent-shaped depressions in the furrows situated between the veins, GP0089, × 5. B, part of GP0089 showing the smaller leaves; the numbers indicate their acropetal order. L indicates impressions of the larger leaves, × 5. C, part of GP0089 showing the arrangement of the crescent-shaped depressions, × 20. D, schematic drawing of part of figure C showing crescent-shaped depressions within a furrow, each depression being down towards the leaf apex. Arrows indicate the positions where stomata are observed normally, × 5. E–G, schematic sections through the crescent-shaped depressions as indicated in D. The thick line represents the compression; hatched area the underlying rock; dotted areas the portions of the sediment trapped in the depression during the splitting of the shale. The arrow in E is directed towards the leaf apex.

arrangement of leaves in *Pterophyllum*. Halle's original diagnosis of *Tingia* was 'Dorsiventral, frond-like anisophyllous shoots with thick axis. Leaves apparently arranged in four rows, two on the upper and two on the lower side of the axis. Leaves of the two rows on one (the upper?) side smaller, directed forward at narrow angle to the axis, those of the other two rows (on the lower side?) larger, spread out in one plane and forming a more open angle to the axis: each lateral half of the shoot thus provided with two rows of dissimilar leaves. Leaves of the larger (normal) type varying from broadly cuneate-obovate to oblong or linear, with entire lateral margins but more or less deeply lobed at the apex. Several veins entering each leaf, dichotomizing mostly in the lower part of the leaf, all branches continuing to the apex.' Originally Halle diagnosed two species—*Tingia carbonica* (Schenk) and *T. crassinervis* sp. nov. Subsequently Halle (1927) added *T. partita* sp. nov. on revising the genus. Previously he had been unsure of the orientation of the shoots, but in 1927 stated that the two ranks of smaller leaves were on the lower side of the shoot. He also pointed out for the first time that the smaller leaves were often deeply dissected.

Konno (1929) described two further species, *T. hamaguchii* and *T. elegans* together with new specimens of *T. partita* and *T.* (cf.) *carbonica* from the Lower Permian of North Korea. He revised Halle's generic diagnosis by adding several new morphological characters. The foliage shoot was shown to become gradually narrower towards the base, while 'contracted at the top into a pointed or bluntly pointed apex'. The axis was 'straight or slightly falcate, unbranched, gradually thinned at the upper and abruptly thickened at the lower end, with several longitudinal striations'. Larger leaves were described as highly variable in form, generally alternate, although sub-opposite in their lower part, and more crowded in the upper region of the shoot. The smaller leaves were generally of a much more regular form.

Other specimens have been described subsequently from the Permian of northern China, the far north of North Korea, and Malaysia. They are *T. laciniata* Kawasaki (1934), *T. kikkawai* Kawasaki (1934), *T. gerardi* Stockmans and Mathieu (1939), *T. trilobata* Stockmans and Mathieu (1939), *T. minor* Konno and Asama (1951), *T. acuminifissa* (Krasser) Bohlin (1971), *T. subcarbonica* Konno, Asama, and Rajah (1971), *T. oblonga*

(Sze) in Gu and Zhi (1974), and *T. yichuanensis* Feng (in Feng *et al.* 1977). However, it is important to realize that amongst these only *T. subcarbonica*, *T. yichuanensis*, and *T. laciniata* were described as having the characteristic four ranks of anisophyllously arranged leaves. Konno *et al.* (1971) did not describe the smaller leaves on their *T. subcarbonica* nor mention them in their diagnosis. Unfortunately, their illustrations are also not convincing enough to prove that the specimens really do possess these smaller leaves. The other species seem to have been included in *Tingia* on the basis of the apparent similarities of their overall appearance to Halle's specimens; that is on the features of their larger leaves.

Similar specimens found outside Asia were described by Darrah (1938) as belonging to *Tingia*. However, these were later shown by Mamay (1968) to be without the two ranks of smaller leaves and he then removed them to his new genus *Russellites*. They were subsequently moved to *Yuania* by Du and Zhu (1982).

There is clearly a difficulty in identifying specimens as *Tingia* when the main generic character of possessing small leaves may be simply concealed by the alignment of the specimens. This problem is returned to later.

Tingiostachya. T. tetralocularis was named by Konno (1929) for some specimens from the Lower Permian of the Jido Series in the far north of North Korea. These specimens, described as reproductive organs, were found associated with either *Tingia hamaguchii* or *T. elegans.* Konno's original diagnosis of the genus was 'Fertile shoot (in the geno-type, *T. tetralocularis*) consists of two parts: a long(?) slender axis and cylindrical terminal cones. Axis slender, forked dichotomously at apex, longitudinally ribbed with small uniform leafy scales. Cone terminal, developed on each of the dichotomized branchlets of the axis, with numerous sporophylls in four vertical series. Sporophylls uniform, more or less elongated, but only slightly modified from the foliage leaf in *Tingia*. A large tetralocular synangium, hemispherical, placed directly on the upper surface of each bract, apart from the cone-axis, receiving one group of bundles from the axis which runs along the median zone of the bract.' Konno described the spore as 'often well preserved, usually of obovate contour, with the larger diameter from 150 μm to 130 μm'.

Another two specimens of *Tingiostachya* have been described by Stockmans and Mathieu (1939) from Kaiping, northern China, although both cones were thought to be specifically indeterminable. The sporophylls of one of these cones (associated with their new foliage species *Tingia trilobata*) seem lobed like the ordinary large leaves of *Tingia*, although they were much smaller and not clearly discernible. Using a pull technique, Stockmans and Mathieu recovered triradiate spores from both cones. These were very similar, about 100 μm in diameter, with smooth surface and said to resemble closely the microspores of *Noeggerathiostrobus* figured by Nemejc (1935).

Examination of the new Taiyuan material has yielded new information that permits a re-evaluation and a rediagnosis of the two genera. Because we have no conclusive evidence that *Tingiostachya* came from the same parent plant as *Tingia* we propose to follow the classification system proposed by Thomas and Brack-Hanes (1984) in their discussion of the lycophytes. They proposed that families should be based on reproductive characters alone, with other organs only included as so-called satellite taxa. This allows a classification system to be constructed to show the most probable relationships between fertile and sterile organs without broadening the family definition to include isolated sterile organs of doubtful affinity. We therefore propose that the family Tingiostachyaceae be used to include the one genus *Tingiostachya*. *Tingia* should be taken as a satellite taxon within the Tingiostachyaceae.

SYSTEMATIC PALAEONTOLOGY

Family TINGIOSTACHYACEAE fam. nov.

Diagnosis. Pedunculate cones with spirally attached sporophylls. Single sporangia attached to proximal part of the adaxial surface of sporophylls with upwardly extended lateral margins (alations).

Genus. Tingiostachya Konno.

Satellite taxon. Tingia Halle.

Genus TINGIOSTACHYA Konno (1929)

Type species. Tingiostachya tetralocularis Konno (1929).

Emended diagnosis. Fertile shoot consisting of a peduncle, with spirally arranged leaves and a terminal cone once dichotomized at its base. Leaves on peduncle ensiform, spirally arranged. Cone

axis slender. Sporophylls spirally arranged, pedicels arising at right angles, with upwardly extending lateral margins (alations). Laminae lanceolate, parallel to cone axis. Sporangia spheroidal, attached to proximal part of adaxial surface of pedicel. Sporangia with small spores.

Tingiostachya tetralocularis Konno (1929)

Plate 89, fig. 10; Plate 90, figs. 1–7; text-fig. 3A–E

1929   *Tingiostachya tetralocularis* Konno, p. 120; pl. XXIII, fig. 5c; pl. XXIV, figs. 4 and 5; pl. XXVII.

Emended diagnosis. Cone about 13·0 cm long, individual cones 8·0–12·0 mm broad. Sporophyll pedicel about 0·5 mm high and 3·0 mm long with upward lateral extensions (alations) about 1·5 mm high. Laminae 5–7·0 mm long, 2–3·0 mm broad. Sporangia 1·0–1·5 mm in diameter. Spores 20 μm in diameter. Peduncle 2–3·0 mm broad; Leaves ensiform about 9·0 mm long and 1·0 mm broad.

Neotype. GP0094, from the Lower Permian, 5 km north-east of East Hill Mine, Taiyuan, Shanxi province, northern China; the whereabouts of the figured specimens of Konno (1929) are unknown (K. Asama, pers. comm.)

Distribution. North Korea: Anji-ri, Daido-gun, S. Heiando (Jido Series and Kobosan Series, Permian). China: East Hill, Taiyuan (Lower Shihezi (Shihhotse) Series, Lower Permian).

Descriptions of new specimens. Those from Taiyuan suggest a rather different morphological interpretation to that proposed by Konno (1929). They are still interpreted as strobili, but their sporophylls are clearly arranged spirally instead of in whorls of four as suggested by Konno. His conclusion that they possessed
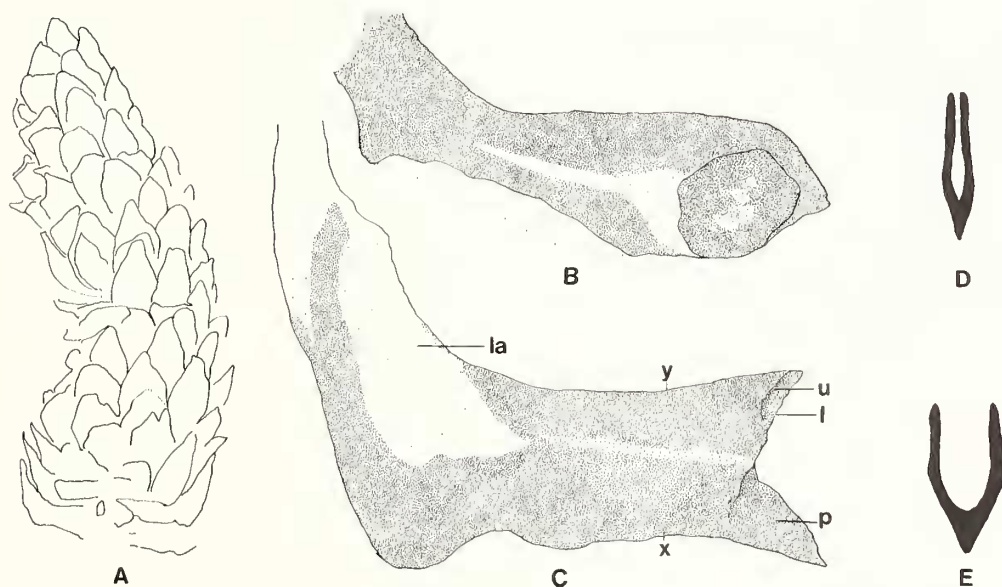
TEXT-FIG. 3. *Tingiostachya tetralocularis* Konno. A, outline drawing showing the apical arrangement of the sporophylls. GP0094, ×2. B, single sporophyll from GP0095 showing a sporangium, ×20. C, single sporophyll from GP0095 showing the two alations (u = upper; l = lower; la = lamina; p = pedicel), ×15. D, schematic cross-section (x–y) of lamina in C showing the compression as embedded in the shale. E, schematic cross section of the same sporophyll, as in life.

their leaves in fours was possibly influenced by the fact that *Tingia* shows four ranks of leaves. It is hard to imagine how the fossilization of an organ having the whorled construction shown by Konno (1929, text-fig. 4A) could possibly result in the appearance of the compression shown in his plate XXIV, fig. 4 and plate XXVII, fig. 2. These photographs show strobili with sporophylls appearing to be in spirals.

Among the new specimens of *Tingiostachya* from Taiyuan, the three most complete show a slender axis, with elongated leaves (Pl. 90, fig. 1), bearing a terminal cone that dichotomizes once just above its base (Pl. 90, figs. 1–3). One shows the cone apex (Pl. 89, fig. 10) to be rounded with the terminal sporophylls gently curved around it. No cone is complete; the longest is 6·8 cm. Their widths are all between 8·0 and 12·0 mm. The axis of the cone is slender, 2–3·0 mm broad and longitudinally ribbed. The sporophylls are all regularly arranged in a spiral on the axis (Pl. 90, fig. 3; text-fig. 3A). Their pedicels are at right angles to the axis and about 3·0 mm long. The laminae turn abruptly upwards to be parallel to the axis and there is a very small heel protruding downwards from the distal end of each pedicel. The laminae are lanceolate-triangular in outline with acute apices, about 6·0 mm long and up to 1·8 mm broad in their basal region, and have entire margins.

Those specimens which are split longitudinally and roughly through the middle reveal certain undescribed features of sporophyll construction. In some laterally compressed sporophylls a layer of light coloured sediment can be seen between two layers of compression material (Pl. 90, fig. 5; text-fig. 3C–E). This suggests that the sporophyll pedicel was not flat, but that its sides were extended and curved upwards. These extensions appear to be approximately equal to, or slightly more than the height of the pedicel. The rounded sporangia (Pl. 90, figs. 4, 6, 7; text-fig. 3B) are about 1·1–1·6 mm in diameter, being probably compressed from an originally spheroidal shape. Each appears to be attached individually to the proximal part of the adaxial surface of a sporophyll pedicel. They were probably protected by the sporophyll alations in life but revealed in the fossil by the splitting of the compression. Scanning electron microscope observation of several impressions of sporangia showed many flattened circular structures which were all approximately 30 μm in diameter. These are interpreted as representing casts, or possibly moulds, of spores. Unfortunately no structural details nor features of surface ornamentation could be seen on any of these putative spores. Some sporangia also possess what appear to represent impressions of the sporangial wall cells. These are about 20 μm broad and radially elongated around the edges of the sporangia.

There are small circular marks on the cone axis which are very similar in size to the sporangia, but are flat and rough in appearance unlike the raised and smooth circles, with concave centres, of the sporangia. They are best interpreted as false pedicel scars formed by the forced removal of the sporophylls during the splitting of the matrix. Judging from the appearance of the present specimens, Konno could have mistaken some of these false scars for sporangia, for he described the sporophylls as having four sporangia, or a tetralocular synangium attached to the upper surface.

Comparisons. The main means of identifying reproductive organs as *Tingiostachya* are the way in which the terminal cones dichotomize once at their very base, their spirally arranged sporophylls, and their spheroidal sporangia attached to the proximal part of the adaxial surface of the sporophyll pedicel. There are no other described genera that can be thought to be closely comparable.

EXPLANATION OF PLATE 89

Figs. 1–9. *Tingia elegans* Konno. 1, GP0087, leafy shoot showing acropetal overlapping arrangement of the deeply lobed larger leaves and their reduction in size towards the base of the shoot, × 2. 2, GP0088, leafy shoot showing basipetal overlapping arrangement of leaves and basal part of the shoot, × 1·5. 3, SEM of a rubber peel of a leaf impression from GP0096 showing the furrows between the veins, × 40. 4, SEM of an amyl acetate peel of the lower surface of a larger leaf compression from GP0097 showing the epidermal cells over a vein, × 200. 5, GP0090, the apical part of a leafy shoot showing size reduction towards the apex of the shoot, × 2. 6, GP0089, leafy shoot showing smaller leaves, × 5. 7, GP0098, a larger leaf showing its toothed upper margin and apex and its dichotomous venation, × 8. 8, GP0046, part of a leafy shoot showing the smaller leaves and the overlapping larger leaves, × 2. 9, SEM of a rubber peel of impression showing a putative stoma on the edge of furrow on the lower surface of leaf from GP0096, × 700.

Fig. 10. *Tingiostachya tetralocularis* Konno, GP0091, the apex of a cone with its spirally arranged and incurved sporophylls, × 10.

PLATE 89

GAO and THOMAS, *Tingia, Tingiostachya*
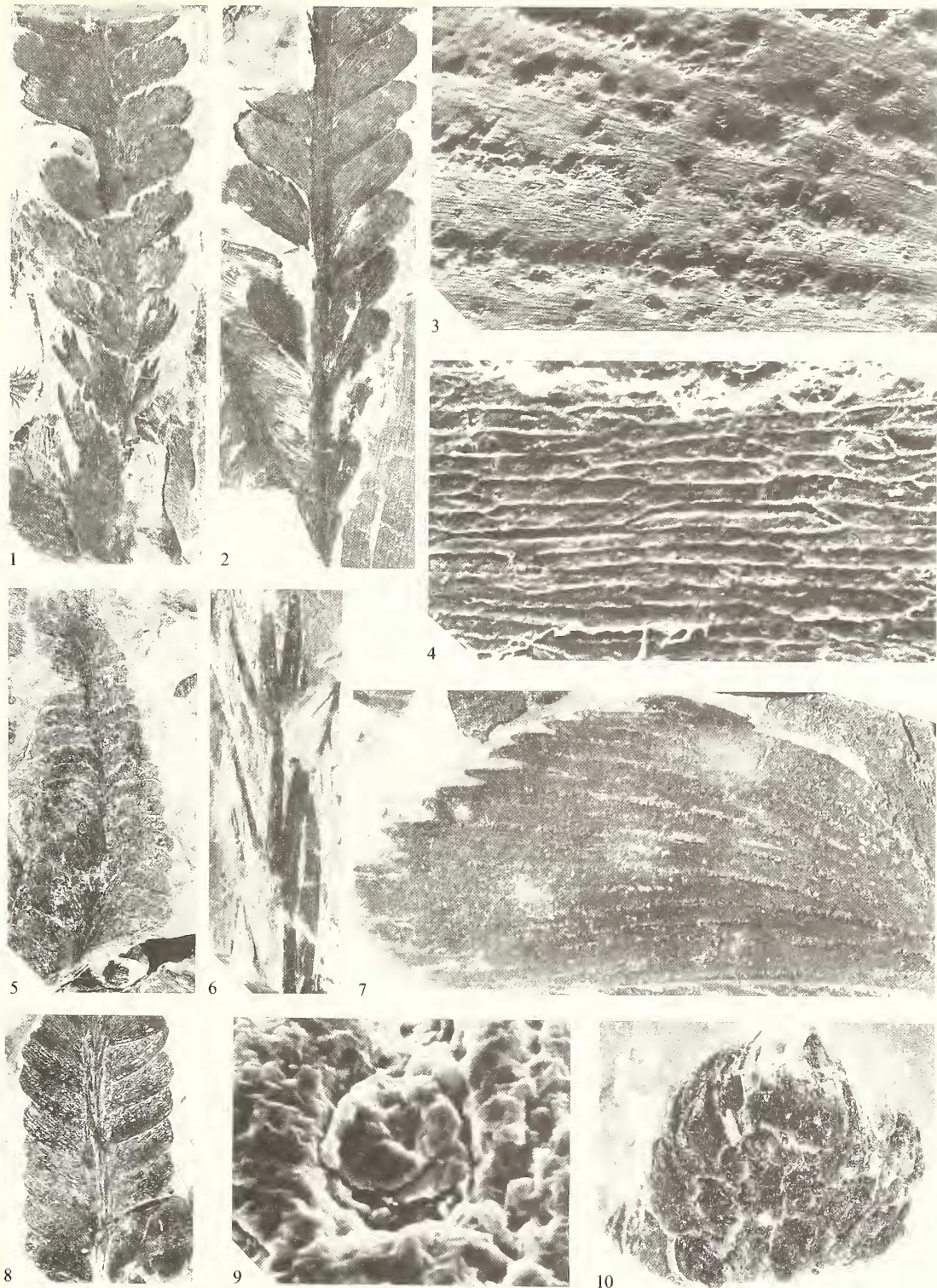
Noeggerathiostrobus Nemejc (1928) has often been thought to be quite similar but this was through the mistaken interpretation that *Tingiostachya* possessed tetralocular synangia. In fact *Noeggerathiostrobus* has a single terminal cone with its bract-like units arranged in semicircular discs around an axis. The sporangia are located on the upper surface of the discs in rows and have been shown to produce two sizes of spores (Nemejc 1928; Halle 1954).

As mentioned earlier, the only named species of the genus is *T. tetralocularis* Konno (1929). As the Taiyuan specimens appear very closely comparable in size and in sporophyll morphology to Konno's figured specimens, we refer them to his species. The specimens of Stockmans and Mathieu (1939, 1957) are much smaller so we prefer to continue to keep them separate.

<div align="center">Genus TINGIA Halle (1925)</div>

Type species. Tingia carbonica (Schenk) Halle (1925)

Emended diagnosis. Dorsiventral, anisophyllous, unbranched foliage shoots; two rows of larger leaves becoming smaller towards apex and base, two rows of smaller leaves. Larger leaves obovate to linear with toothed apical margins and decurrent bases, alternately arranged on axis, spreading; veins dichotomizing, ending in marginal teeth. Smaller leaves almost parallel to shoot axis.

<div align="center">*Tingia elegans* Konno (1929)</div>

<div align="center">Plate 89, figs. 1–9; text-fig. 2A–G</div>

Emended diagnosis. Larger leaves obovate, about 10 mm long and 6 mm broad; apex rounded with teeth about 1 mm long; lower margin straight with decurrent base; veins dichotomize twice or more. Epidermal cells longitudinally elongate along the veins and approximately 100 μm long and 15 μm wide. Stomata visible on edges of veins, approximately 25 μm long and 20 μm broad. Smaller leaves about 4 mm long, 1 mm wide.

Neotype. GP0087, from the Lower Permian, 5 km north-east of East Hill Mine, Taiyuan, Shanxi province, northern China. The whereabouts of the figured specimens of Konno (1929) are unknown (K. Asama, pers. comm. 1986).

Distribution. Riajin-ri, Daido-gun, south Heiando, North Korea (Jido Series and Kobosan Series, Permian). East Hill, Taiyuan, China (Lower Shihezi Series, Lower Permian) and all the other localities indicated for the genus on the accompanying map.

Descriptions of new specimens. About forty specimens collected by Gao from the East Hill region of Taiyuan were studied. Most are compressions with many lacking their counterpart impressions. Unfortunately all are fragmentary with only one showing an apex (Pl. 89, fig. 5) and three their basal regions (Pl. 89, figs. 1 and 2). The longest fragment of shoot is 12 cm, although we estimate their original lengths to be in the order of 20 cm or more. The axes are longitudinally striated and vary in width from 1 mm to 3 mm in different specimens. The shoots are dorsiventral and anisophyllous with two ranks of larger leaves and two ranks of much smaller leaves (Pl. 89, figs. 6 and 8).

It is difficult to see the arrangements of both kinds of leaves on most specimens. There are two ways in which the larger leaves overlap each other on the shoot. If the overlapping is directed towards the apex

<div align="center">EXPLANATION OF PLATE 90</div>

Figs. 1–7. *Tingiostachya tetralocularis* Konno. 1, GP0093, a once dichotomized, longitudinally split cone on its leafy pedicel, × 1·5. 2, GP0093, a once dichotomized cone on its leafy pedicel, × 2. 3, GP0094, a once dichotomized cone showing its spirally arranged lanceolate sporophylls, × 2. 4, GP0093, single sporangium, × 30. 5, GP0095, single isolated sporophyll (drawn as text-fig. 3c), × 10. 6, GP0095, single sporophyll with a sporangium (drawn as text-fig. 3B), × 10. 7, GP0094, part of sporangium hidden under the overlapping compression of the sporophyll alation, × 20.

PLATE 90

GAO and THOMAS, *Tingiostachya*
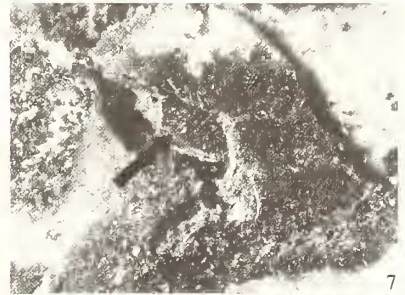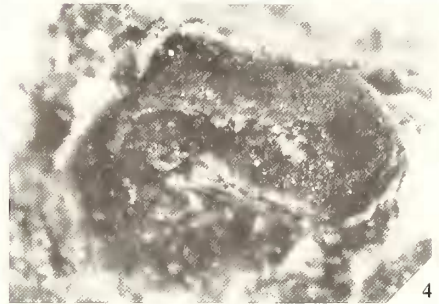
(Pl. 89, fig. 1), that is with the lower margin of each leaf being hidden by the upper margin of the subsequent leaf, the smaller leaves are angled down into the matrix where they are hidden unless uncovered. In those specimens where the overlapping is directed towards the base the smaller leaves are directed upwards. However, only one specimen has been found that shows both types of leaves in this arrangement (Pl. 89, fig. 8). Most have lost their smaller leaves which were ripped off with the counterpart portion of matrix during the splitting of the shale (Pl. 89, fig. 2).

The larger leaves are usually obovate, sometimes slightly elongate in form, with their oblique and decurrent bases attached to the axis by short petioles. The length of the larger leaves varies from 8 to 15 mm and the median width from 4 to 7 mm in different specimens. The angle of the lower leaf margin to the axis varies from 40° to 80°; being constant within a specimen but varying between them. Occasionally the two ranks are attached at different angles, although we attribute this to compression effects during preservation. The lower margin of the leaves are straight and the upper margins somewhat semicircular. The apical portion of the upper margin and the rounded apex are toothed with the longest teeth in the former area (Pl. 89, fig. 7). The veins are usually dichotomizing and terminate either singly, or very occasionally in pairs, in the marginal teeth. There are about ten to eighteen veins in the broadest part of the leaf and about the same number or slightly more reach the margin.

The splitting of the shale has resulted in two basic kinds of specimens. One shows the larger leaves as dark compressions with either discontinuous light furrows and/or more occasionally discontinuous light or dark ridges. The other kind show the larger leaves as impressions with discontinuous light ridges and/or light or dark furrows running along their length. These latter ridges and furrows equate to those visible on those leaves preserved as compressions. These furrows are positioned between the veins and are most obvious in the middle and apical parts of the leaves. (Pl. 89, fig. 3; text-fig. 2A). Distinctive features have been observed in the furrows of some specimens in which the leaves overlap each other towards the apex. These furrows consist of many closely packed but individual depressions; each being crescent-shaped with its convex side directed towards the leaf apex (text-fig. 2A, C, D). These crescent-shaped depressions are also angled down towards the leaf apex (text-fig. 2 E–G) and very occasionally they are joined together in the middle. Scanning electron microscope observations of epoxy and rubber pulls from impressions of the leaves show epidermal cell outlines (Pl. 89, fig. 4) that are longitudinally elongated along the veins and about 50–150 μm long and 8–32 μm wide. Stomata are also visible on the sides of the furrows, that is on the very edges of the well-preserved veins. We suspect that there were many stomata in the crescent-shaped depressions, but the retention of quantities of rock matrix in these depressions prevents us from making the necessary observations. The probable guard cell-like structures (Pl. 89, fig. 9) that can be seen are about 25 μm long and 10 μm broad. Regular hollows, mostly in the furrows, that have similar sizes to the stomata are most probably evidence of stomata in which the guard cells were not preserved.

The smaller leaves are ensiform with tapering margins, 7 mm long, 1–2 mm wide, and directed apically along the axes (Pl. 89, figs. 6 and 8; text-fig. 2B).

The basal part of the shoot shows a rather different arrangement to the main leafy part. The larger leaves become basipetally smaller and are arranged more acutely to the axis. The smallest are 3·0 mm long, 1·5 mm broad, and dissected into three lobes, thereby appearing very similar to the smaller leaves in both size and shape.

Comparisons. The generic identification of *Tingia* is based on the dorsiventral and anisophyllous arrangement of its shoots with two ranks of larger leaves on one side of the shoot and two ranks of much smaller leaves on the other. The toothed apex and apical part of the upper margin of the larger leaves and the numerous dichotomizing veins that terminate in the teeth are also characteristic features. The outwardly similar genera *Noeggerathia* Sternberg, *Russellites* Mamay, and *Plagiozamites* Zeiller with their dorsiventrally flattened large leaves are not anisophyllous as they possess no ranks of smaller leaves. As the new Taiyuan specimens are both dorsiventral and anisophyllous they clearly belong to *Tingia*.

Fifteen species of *Tingia* have been described to date, excluding the two removed by Mamay to *Russellites*. However, only eight are known to have the anisophyllous arrangement of four ranks of leaves. The morphological details of all fourteen species are summarized in Table 1 as described by their authors. The closest comparable species to the new specimens are *T. hamaguchii* Konno (1929), *T. partita* Halle (1927), and *T. elegans* Konno (1929).

T. hamaguchii has similar shaped leaves to the new specimens although they are about twice the size. It also has a looser leaf arrangement (about 1 leaf per cm instead of 1·3–3 leaves per cm as

TABLE 1. Comparison of the species of *Tingia*.

| | Characters | | | | | | | |
| | Shoot | | Larger leaves | | | | | |
	Total width (mm)	Width of axis (mm)	Angle to the axis	Shape	Length (mm)	Width (mm)	Apex	Number of veins in the middle of the leaf
Species described with four ranks of leaves								
T. carbonica (1)	60–75	3–8	40–60	oblong-linear	100	10	truncate	12–24
T. crassinervis (1)	110–130*	10	40–60	oblong-linear	>90*	20*	obtuse	20
T. partita (2)	40–45	5	50–60	obcuneiform	20–25	10	truncate	?
T. hamaguchii (3)	20–30	2	40–50	obtetragonal	15–30	7*	obtuse*	18–24
T. elegans (3)	17–24	1–1.5	30–60	obovate	10–16	10	rounded	13–15
T. laciniata (4)	>120*	4*	45*	lanceolate	50	10	obtuse*	25
T. subcarbonica (5)	>275*	10–15	60	broadly linear	130	25	truncate	60
T. yichuanensis (10)	30*	2	55	obovate	13	7	rounded	18
Species described with no reference to the smaller leaves								
T. kikkawai (4)	?	?	?	elliptical	20–30	10–12	?	?
T. gerardii (6)	17–24	2*	45*	obovate	12–15	14*	rounded*	?
T. trilobata (6)	30–40*	5	45	triangular	25–30	9*	truncate	?
T. minor (7)	5–7	1	30–40	obovate	4–5	2*	rounded	?
T. oblonga (8)	20*	1	60–70	oblong	10	5	obtuse	?
T. multidentata (9)	5–7	3.5	50	triangular	15	8	obtuse*	?
T. acuminifissa (9)	30*	3	40*	triangular	15*	7*	truncate*	?
Present specimens	11–26	1–3	40–80	obovate	8–15	4–7	rounded	10–18

(1) Halle 1925. (2) Halle 1927. (3) Konno 1929. (4) Kawasaki 1934. (5) Konno *et al.* 1971. (6) Stockmans and Mathieu 1939. (7) Konno and Asama 1951. (8) Gu and Zhi 1974. (9) Bohlin 1971. (10) Feng *et al.* 1977.
* Not mentioned in published description, data from photographs.

in the Taiyuan specimens) and the leaves are more closely aligned to the axis (their lower margins being at 25°-50° instead of the 40°-80° in the Taiyuan specimens). *T. partita* differs from the present specimens in having larger and more triangular-shaped leaves with more divergent veins and deeply dissected apices that are most closely comparable to *T. elegans* (which was included as a synonym of *T. hamaguchii* by Lee *et al.* (Gu and Zhi 1974)), and in having similar leaf morphologies and leaf densities (Konno's specimens average 2 leaves per cm). The figures of Konno's earlier specimens seem to show more elongated leaves (Konno 1929, pl. XXV, figs. 1-8), whereas Konno and Asama's later specimens appear virtually identical to ours (Konno and Asama 1951, pl. 9, figs. 5-7). The differences in appearance of the leaf shape of Konno's original specimens can be interpreted as due to the different manner of leaf overlap. Here it is the upper margin which is hidden by the leaf above, thereby producing an elongated appearance to the otherwise obovate leaf.

DISCUSSION

Tingia and *Tingiostachya* have been classified in various ways by different authors. This has resulted from the varied interpretations and preferred emphasis of vegetative or reproductive characters. Furthermore, it has been generally assumed that the two organs came from the same parent plant because of their consistent association at different sites, even though they have never been found in organic attachment to each other or to any other organ. Indeed, as they have never been found other than as isolated organs we have no knowledge of the overall morphology of the parent plant.

Halle (1925) proposed *Tingia* to be an aquatic plant with the two ranks of larger leaves floating on the surface and the two smaller leaves submerged. Konno rejected Halle's proposal, suggesting instead that *Tingia* grew in the same manner as extant *Selaginella* and *Lycopodium* although he did note that it was much larger and never branched. He concluded that *Tingia* shoots were most probably foliage branches given off laterally or almost horizontally on the ground from a creeping stem.

From the morphological characters of the Taiyuan specimens we conclude that they represent long shoots, rather than pinnate frond-like organs, that were shed from woody plants. They were most likely to have been orientated with their smaller leaves uppermost as in the anisophyllous species of *Selaginella*. This we deduce from the fact that it is the surfaces of the larger leaves furthest away from the smaller leaves that have the crescent-shaped grooves. If these really are stomatal grooves then they are virtually certain to have been on the underside of the leaves. The larger leaves also appear to be quite thick and this together with their possession of 'stomatiferous' crescent-shaped depressions suggests that they were quite fleshy. Furthermore, it can be taken to suggest that the plants were growing in a relatively dry environment.

Halle (1927) suggested that there was a close relationship between the genera *Tingia*, *Noeggerathia*, and *Plagiozamites*. He therefore proposed that *Tingia* be used as the basis for the family Tingiaceae that included these three genera. Halle of course had found no reproductive organs. Konno compared *Tingiostachya* with the Sphenophyllales and Lycopodiales before classifying it with the extant Psilotaceae on account of the presumed tetralocular synangia even though he noted several major morphological differences. Nemejc (1931) subsequently rejected Konno's interpretations of the plant's affinity and followed Halle in grouping *Tingia*, *Noeggerathia*, and *Plagiozamites* together on the basis of common foliage organization, but placed them in the Noeggerathiales instead of using the family Tingiaceae.

Browne (1933) suggested the affinities of *Tingia* and *Tingiostachya* should lie with the Sphenophyllales. This was based on the supposed verticillate arrangement of the sporophylls in *Tingiostachya* and that the leaves of *Tingia* were similar to the undivided wedge-shaped leaves of the Euramerian genus *Sphenophyllum*. Browne also suggested that the Psilotales should be included in the Sphenopsida.

Stockmans and Mathieu (1939, 1957) and Lee (1963) did not attempt to put either *Tingia* or *Tingiostachya* into a family but included them both as *incertae sedis*.

Most recent accounts accept some relatively close relationship between *Tingia*, *Tingiostachya*, and *Noeggerathia*, although there is differing opinion on their classifications. Boureau (1964) includes the Tingiales (*Tingia* and *Tingiostachya*) in the Noeggerathiophytina. Bohlin (1971) and Lee *et al.* (*in* Gu and Zhi 1974) both take a wide view of the Noeggerathiales as containing *Tingia* and several other leaf genera including *Plagiozamites*, *Yuania*, and *Concophyllum*. Lee *et al.* (Gu and Zhi 1974) also included the reproductive genus *Discinites* and Bohlin (1971) the other leaf genus *Ginkgophyllum*. Taylor (1981) merely points out the similarity between *Tingia* and *Noeggerathia* and includes them both in the progymnosperms. Beck (1981) suggested a relationship between *Tingia*, *Noeggerathia*, and *Archaeopteris* including the former two in the Noeggerathiopsida.

Both *Tingia* and *Tingiostachya* appear to us to suggest a quite unique plant; assuming of course that they really did belong to the same parent plant. We do not accept that there can be any meaningful classification system established on the basis of rather broad similarities of vegetative organs. Neither do we believe that there is any close relationship between *Noeggerathiostrobus* and *Tingiostachya* as we have reinterpreted it here. Indeed, we cannot even say if the parent plant was a pteridophyte, a gymnosperm, or even a progymnosperm.

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